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Research Article

Updated checklist, habitat affinities, and changes over time of the Indiana (USA) caddisfly fauna (Insecta, Trichoptera)

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Abstract

Based on recent collecting and a synthesis of ~100 years of historical data, 219 caddisfly species are reported from the state of Indiana. Seventeen species are reported herein from the state for the first time, including two previously thought to be endemic to the southeastern USA. Species records are also presented herein organized by drainage basin, ecoregion, glacial history, and waterbody type for two distinct time periods: before 1983 and after 2005. More species were reported from the state before 1983 than after 2005, despite collecting almost 3× the number of occurrence records during the latter period. Species occurrence records were greater for most families and functional feeding groups (FFGs) for the post-2005 time period, although the Limnephilidae, Phryganeidae, Molannidae, and Lepidostomatidae, particularly those in the shredder FFG, instead had greater records before 1983. This loss of shredders probably reflected the ongoing habitat degradation within the state. While species rarefaction predicts only a few more species to be found in Indiana, many regions still remain under-sampled and 44 species have not been collected in >40 years.

Key words: Biological diversity, conservation, distribution, insect, Upper Midwest

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Introduction

The caddisflies (Trichoptera) constitute an important group of aquatic organisms due to their high overall abundance, high species richness, high ecological diversity, and differing sensitivities to various anthropogenic disturbances (Barbour et al. 1999; Morse et al. 2019). Determining caddisfly distributions and habitat affinities, therefore, is valuable for assessing water quality and other aspects of ecosystem integrity (Dohet 2002; Houghton and DeWalt 2021). Assessing changes in such data over time can be especially valuable (Houghton and Holzenthal 2010).

The caddisflies of the Upper Midwest region of the United States (MAFWA 2023) have been studied for nearly 100 years, starting with the Illinois fauna (Ross 1938, 1944), including more recent comprehensive studies of Kentucky (Floyd et al. 2012), Michigan (Houghton et al. 2018, Minnesota (Houghton 2012), Missouri (Moulton and Stewart 1996), Ohio (Armitage et al. 2011), and Wisconsin (Hilsenhoff 1995), and culminating with an overall checklist of the entire region (Houghton et al. 2022). The last paper included 131 new state spe-

cies records combined from eight different states, including five from Indiana, demonstrating that even well-collected areas still contain undiscovered species.

Research on the Indiana caddisfly fauna encompasses two approximate time periods. The first period began in the 1930s and concluded with Waltz and McCafferty's (1983) checklist of 190 species. Specimens from this period are housed primarily in the Purdue University Entomological Research Collection (PERC) and the Illinois Natural History Survey Insect Collection (INHS). After a ~20-year pause, caddisfly collecting renewed in the early 2000s with subsequent studies by DeWalt et al. (2016a) and Bolton et al. (2019), as well as many specimens accessioned into the PERC, INHS and, more recently, the Hillsdale College Insect Collection (HCIC). This nearly 100-year collecting history provided an opportunity to assess any changes in the caddisfly fauna over time.

Indiana is composed of a single USEPA Level I ecoregion and three secondary ecoregions: Central Plains, Mixed Wood Plains, and Southeastern Plains (Fig. 1). The predominant land use is agriculture in the form of row crops and pasture, especially in the northern two thirds of the state. Land use corresponds strongly with glacial history, as the low-gradient environments and abundant glacial till of the more recent Wisconsin glaciation are more conducive to farming than the higher-gradient and more eroded older landscapes of the Illinoian glaciation and unglaciated regions.

The primary objective of this study was to update the state caddisfly checklist for Indiana and relate the occurrences of all species to drainage basin, ecoregion, glacial history, and waterbody type. We also assessed the rarity of all Indiana species. Since >40 years had passed since the last state checklist, we assessed any notable changes to the fauna during this period. Further, we used species rarefaction to predict total species richness for the state and assessed the importance of collecting effort on a regional level.

Materials and methods

Our primary sampling devices included two types of ultraviolet light traps: an unattended 8-watt light placed over a white pan filled with ethanol, and an attended 12-watt light suspended from a white sheet with two pans filled with ethanol at its base. Such devices were set out at dusk near aquatic habitats and retrieved approximately two hours later (Houghton 2004; Wright et al. 2013; DeWalt et al. 2016a). The nocturnally active caddisfly adults were attracted to the lights and either fell into the pan or were hand-collected (Fabian et al. 2024). Sampling the winged adults is necessary for taxonomic and conservation studies since, unlike larvae, they are usually identifiable to the species level. Moreover, since adults are attracted to lights irrespective of their specific natal microhabitat or functional feeding group (FFG), inferences on ecology and biotic integrity can be made about an ecosystem without the sampling bias that affects benthic studies (Cao and Hawkins 2011). We and our colleagues collected 194 of these ultraviolet light samples from 2005–2023 (Fig. 2, Suppl. material 1). We also data-based specimens from the INHS and PERC going back to the early 1900s. These specimens represented collections of unknown effort. Thus, Fig. 2 makes the distinction between "collections" (unknown effort) and "samples" (the ultraviolet light sampling regime described above). All specimens are housed in either the HCIC, INHS, or PERC institutional collection.

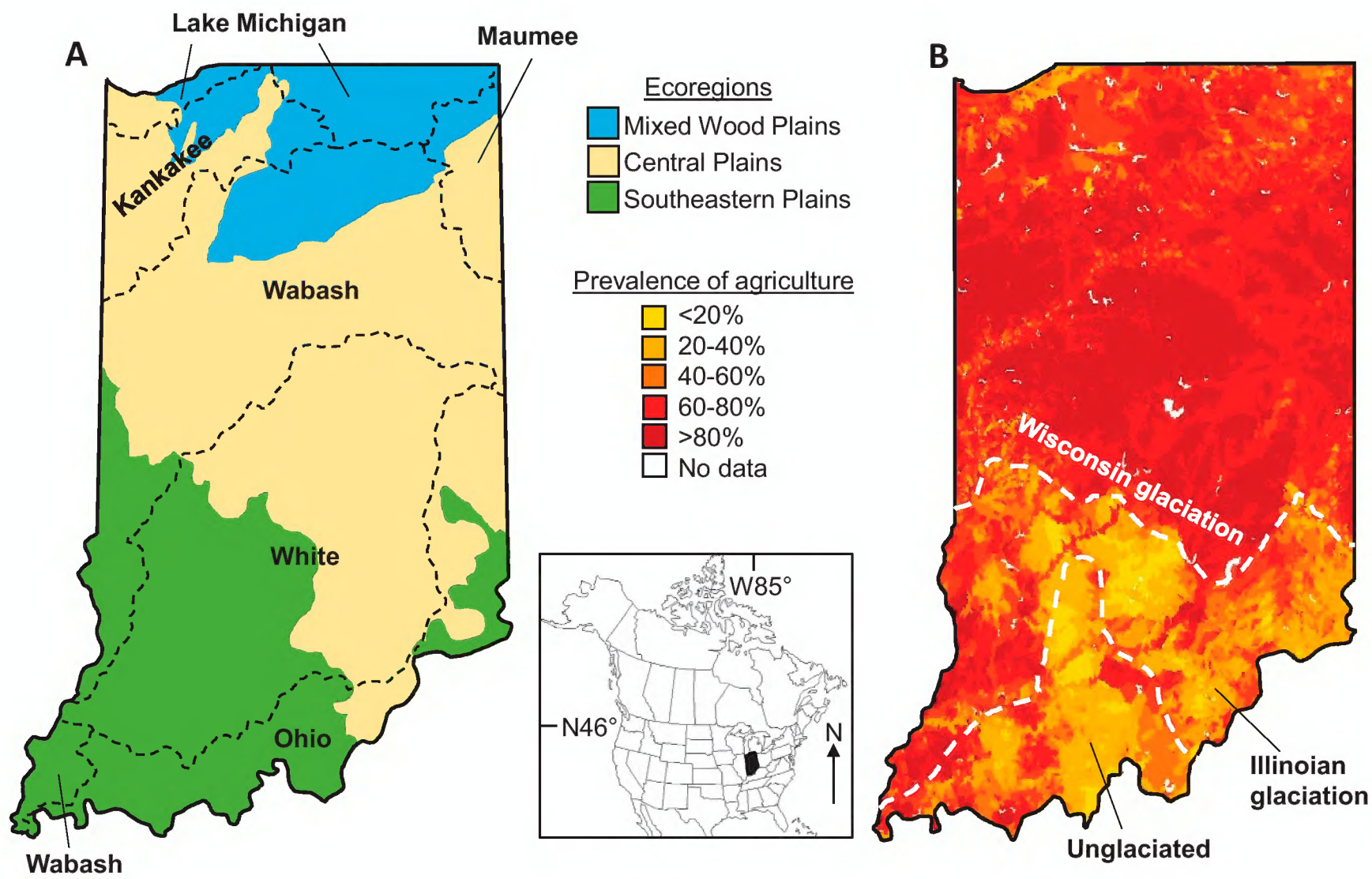

Figure 1. Location of the state of Indiana showing the approximate boundaries of drainage basins and ecoregions (**A**), and prevalence of agriculture and Pleistocene glacial history (**B**).

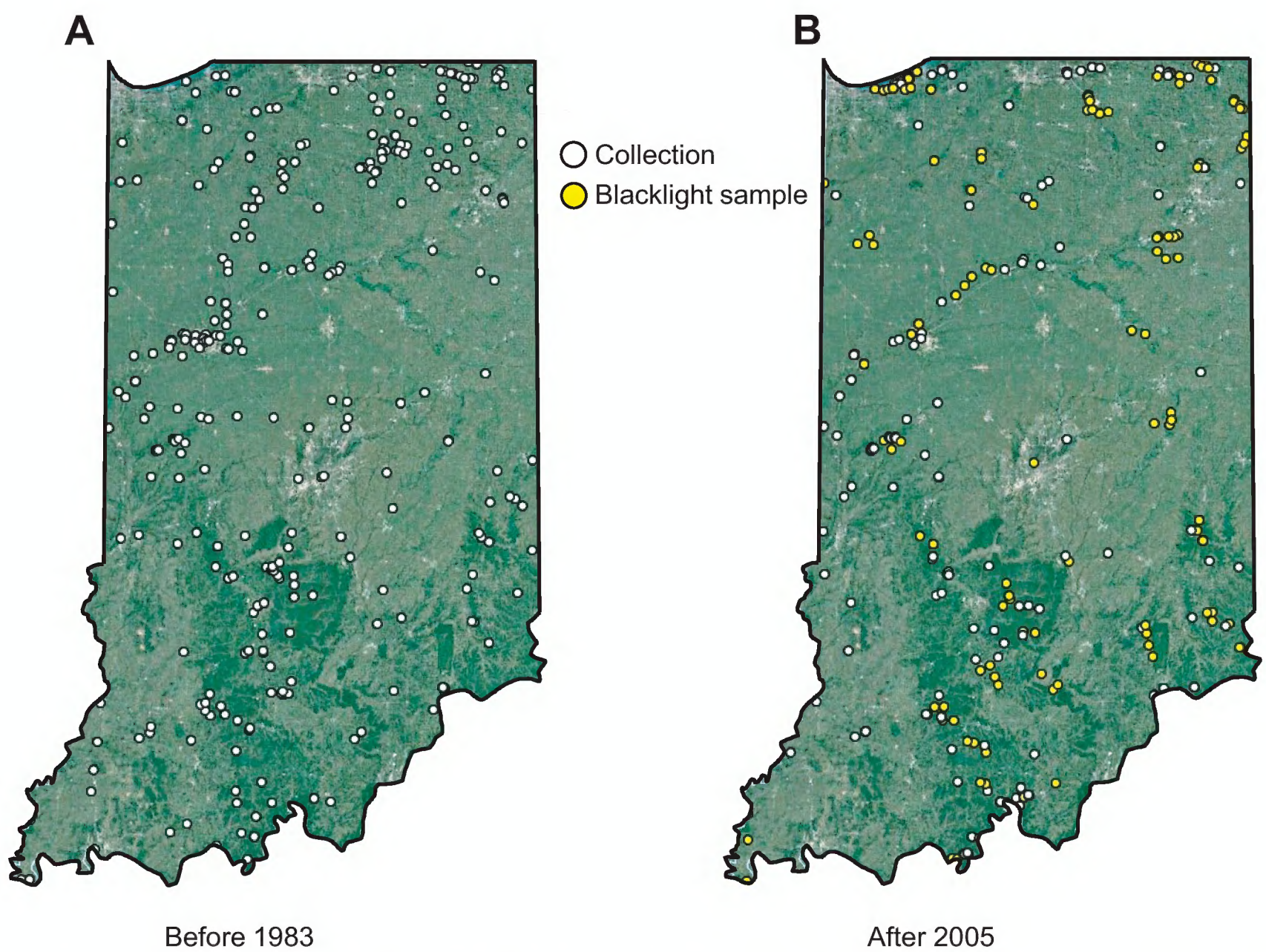

Figure 2. Collecting localities of Indiana caddisflies before 1983 (**A**) and after 2005 (**B**). White markers represent collections of unknown sampling effort whereas yellow markers represent ~2 h ultraviolet blacklight samples. Base map © Google, NOAA.

We associated all 1116 unique collecting localities with drainage basin, ecoregion, glacial maximum, and waterbody type. Our approach for dividing the state into geographic and ecological regions was a balance between having divisions specific enough to reflect biological differences, yet large enough to maintain a consistent collecting effort between them. Thus, we divided the state by United States Environmental Protection Agency Level II ecoregions (https://www.epa.gov/eco-research/ecoregions-north-america) and Hydrologic Unit Code (HUC) 6 drainages (https://water.usgs.gov/GIS/huc.html). For the latter we combined smaller watersheds with a common outlet (e.g., the various HUC6 drainages all draining into the Ohio River) into their larger drainages (Fig. 1). While slightly nonstandard, we prefer this categorization over attempting to compare small drainages with minimal collecting effort to those with hundreds of collections. We also divided the state based on glacial maximum (Gray and Letsinger 2011). Lastly, we categorized specific sampling sites by lake or size of stream (https://www.epa.gov/waterdata).

To estimate total species richness for the state, a species rarefaction curve based on all species and samples collected was produced using the program EstimateS for Windows v. 9.1 (https://www.robertkcolwell.org/pages/estimates). In addition to the basic curve, two maximum species richness estimators were calculated. The abundance-based coverage estimator (ACE) predicted total species richness based on a proportion of rare to common species, defining "rare" as any species represented by <10 specimens. The incidence-based coverage estimator (ICE) made the same prediction, but defined "rare" as any species found in <10 samples.

To assess the importance of sampling effort in collecting species, simple linear regression models were calculated for the number of species collected from each of the primary watershed, ecoregion, glacial maximum, and waterbody type designations (dependent variable) based on the accumulated number of unique collections and samples combined (independent variable). Separate models were calculated for the pre-1983 and post-2005 time periods. The number of species associated with each geographic and habitat designation was treated as an independent observation even though each sample or collection was associated with designations of all four types.

Results

A total of 219 caddisfly species among 18 families and 62 genera were determined to occur in the state of Indiana, including 17 species reported for the first time herein (Table 1). An additional seven species were removed from the state checklist due to misidentified specimens, taxonomic changes, or dubious identifications lacking voucher specimens (Table 2). The determined species are based on 80,298 total specimens representing 5223 species occurrence records from 711 unique collecting events before 1983 and 405 events after 2005 (Suppl. material 1). Because a detailed taxonomic history, including all synonymies, and regional distributions of all 219 species have already been treated in Houghton et al. (2022) and Rasmussen and Morse (2023), we do not reproduce those data herein.

Of the known species, 100 (46%) were considered abundant or common, whereas 75 (34%) were considered rare, and 44 (20%) have not been collected in the last 40 years and, thus, were considered data deficient (Table 1). Leptoceridae (43 species), Hydroptilidae (42), and Hydropsychidae (38) were the most

species rich families. They were also the families with the greatest number of total species occurrence records, collectively encompassing nearly 75% of all such records (Fig. 3). Species found only either before 1983 or after 2005 occurred in similar proportions for most families. The exceptions were the Limnephilidae and Phryganeidae, which collectively included 11 species found only before 1983 and none found only after 2005 (Fig. 4). The genera *Fabria*, *Oligostomis* (both Phryganeidae), and *Hydatophylax* (Limnephilidae) were found only before 1983, whereas *Ithytrichia* and *Leucotrichia* (both Hydroptilidae) were found only after 2005.

Table 1. The 219 caddisfly species known to occur in Indiana based on all historical and contemporary collecting and sampling. All taxa are arranged alphabetically by order and family. Species reported from the state for the first time are in boldface font. Species records displayed based on those found before 1983 and after 2005. Rarity designation based on number of records after 2005: >20 = abundant, 6–20 = common, 1–5 = rare, 0 = data deficient to determine if the species still exists in the state. Most recent known collection year of data-deficient species are in the last column.

	Records before 1983	Records after 2005	Rarity	Most recent
BRACHYCENTRIDAE (5)				
Brachycentrus lateralis (Say, 1823)	1	0	Deficient	1903
Brachycentrus numerosus (Say, 1823)	9	4	Rare	–
Micrasema rusticum (Hagen, 1868)	3	4	Rare	–
Micrasema scotti Ross, 1947	2	0	Deficient	1977
***Micrasema wataga* Ross, 1938**	**0**	**2**	**Rare**	–
DIPSEUDOPSIDAE (2)				
Phylocentropus lucidus (Hagen, 1961)	1	0	Deficient	1980
Phylocentropus placidus (Banks, 1905)	3	6	Common	–
GLOSSOSOMATIDAE (11)				
Agapetus gelbae Ross, 1947	2	0	Deficient	1946
Agapetus illini Ross, 1938	1	2	Rare	–
***Agapetus spinosus* Etnier & Way, 1973**	**0**	**1**	**Rare**	–
Glossosoma intermedium (Klapálek, 1892)	3	2	Rare	–
Glossosoma nigrior Banks, 1911	1	6	Common	–
Protoptila erotica Ross, 1938	1	13	Common	–
***Protoptila georgiana* Denning, 1948**	**0**	**1**	**Rare**	–
***Protoptila lega* Ross, 1941**	**0**	**1**	**Rare**	–
Protoptila maculata (Hagen, 1861)	7	36	Abundant	–
Protoptila palina Ross, 1941	1	0	Deficient	1948
Protoptila tenebrosa (Walker, 1852)	1	0	Deficient	1936
GOERIDAE (1)				
Goera stylata Ross, 1938	1	1	Rare	–
HELICOPSYCHIDAE (1)				
Helicopsyche borealis (Hagen, 1861)	30	59	Abundant	–
HYDROPSYCHIDAE (38)				
Cheumatopsyche analis (Banks, 1908)	44	111	Abundant	–
Cheumatopsyche aphanta Ross, 1938	3	4	Rare	–
Cheumatopsyche burksi Ross, 1941	2	17	Common	–
Cheumatopsyche campyla Ross, 1938	37	103	Abundant	–
Cheumatopsyche lasia Ross, 1938	1	1	Rare	–
Cheumatopsyche minuscula (Banks, 1907)	1	0	Deficient	1957
Cheumatopsyche oxa Ross, 1938	24	58	Abundant	–
Cheumatopsyche pasella Ross, 1941	9	49	Abundant	–
Cheumatopsyche sordida (Hagen, 1861)	4	15	Common	–
Cheumatopsyche speciosa (Banks, 1904)	7	2	Rare	–
Diplectrona metaqui Ross, 1970	2	3	Rare	–
Diplectrona modesta Banks, 1908	26	18	Common	–

	Records before 1983	Records after 2005	Rarity	Most recent
Homoplectra doringa (Milne, 1936)	3	3	Rare	–
Hydropsyche aerata Ross, 1938	6	6	Common	–
Hydropsyche alternans (Walker, 1852)	2	0	Deficient	1951
Hydropsyche arinale Ross, 1938	1	1	Rare	–
Hydropsyche betteni Ross, 1938	31	88	Abundant	–
Hydropsyche bronta Ross, 1938	17	71	Abundant	–
Hydropsyche cheilonis Ross, 1938	14	31	Abundant	–
Hydropsyche cuanis Ross, 1938	8	8	Common	–
Hydropsyche depravata Hagen, 1861	5	11	Common	–
Hydropsyche dicantha Ross, 1938	9	10	Common	–
Hydropsyche frisoni Ross, 1938	4	11	Common	–
Hydropsyche hageni Banks, 1905	1	0	Deficient	1950
Hydropsyche incommoda Hagen, 1861	44	68	Abundant	–
Hydropsyche morosa Hagen, 1861	43	7	Common	–
Hydropsyche phalerata Hagen, 1861	13	23	Abundant	–
Hydropsyche placoda Ross, 1941	0	1	Rare	–
Hydropsyche scalaris Hagen, 1861	5	5	Rare	–
Hydropsyche simulans Ross, 1938	27	66	Abundant	–
Hydropsyche slossonae Banks, 1905	8	8	Common	–
Hydropsyche sparna Ross, 1938	17	58	Abundant	–
Hydropsyche valanis Ross, 1938	8	1	Rare	–
Macrostemum carolina (Banks, 1909)	10	11	Common	–
Macrostemum transversum (Walker, 1852)	2	1	Rare	–
Macrostemum zebratum (Hagen, 1861)	14	11	Common	–
Potamyia flava (Hagen, 1861)	46	92	Abundant	–
HYDROPTILIDAE (42)				
Agraylea multipunctata Curtis, 1834	5	12	Common	–
Dibusa angata Ross, 1939	1	0	Deficient	1950
Hydroptila ajax Ross, 1938	2	19	Common	–
Hydroptila albicornis Hagen, 1861	1	2	Rare	–
Hydroptila amoena Ross, 1938	1	0	Deficient	1976
Hydroptila angusta Ross, 1938	8	66	Abundant	–
Hydroptila armata Ross, 1938	7	77	Abundant	–
Hydroptila consimilis Morton, 1905	6	56	Abundant	–
Hydroptila delineata Morton, 1905	2	0	Deficient	1937
Hydroptila grandiosa Ross, 1938	5	53	Abundant	–
Hydroptila gunda Milne, 1939	0	10	Common	–
Hydroptila hamata Morton, 1905	1	26	Abundant	–
Hydroptila jackmanni Blickle, 1963	1	0	Deficient	1976
Hydroptila perdita Morton, 1905	10	72	Abundant	–
Hydroptila scolops Ross, 1938	0	2	Rare	–
Hydroptila spatulata Morton, 1905	3	16	Common	–
Hydroptila vala Ross, 1938	1	0	Deficient	1976
Hydroptila waubesiana Betten, 1934	16	128	Abundant	–
***Ithytrichia clavata* Morton, 1905**	**0**	**4**	**Rare**	–
***Leucotrichia pictipes* (Banks, 1911)**	**0**	**1**	**Rare**	–
Mayatrichia ayama Mosely, 1937	1	1	Rare	–
Neotrichia minutisimella (Chambers, 1873)	1	1	Rare	–
Neotrichia okopa Ross, 1939	0	1	Rare	–
***Neotrichia vibrans* Ross, 1938**	**0**	**3**	**Rare**	–
Ochrotrichia eliaga (Ross, 1941)	3	0	Deficient	1975
Ochrotrichia riesi Ross, 1944	1	0	Deficient	1945
Ochrotrichia tarsalis (Hagen, 1861)	6	26	Abundant	–
Ochrotrichia wojcickyi Blickle, 1963	1	0	Deficient	1980
Ochrotrichia xena (Ross, 1938)	3	0	Deficient	1976

	Records before 1983	Records after 2005	Rarity	Most recent
Orthotrichia aegerfasciella (Chambers, 1873)	5	63	Abundant	–
***Orthotrichia baldufi* Kingsolver & Ross, 1961**	**0**	**2**	**Rare**	–
Orthotrichia cristata Morton, 1905	5	43	Abundant	–
Oxyethira coercens Morton, 1905	2	2	Rare	–
Oxyethira dualis Morton, 1905	0	1	Rare	–
Oxyethira forcipata Mosely, 1934	1	19	Common	–
Oxyethira grisea Betten, 1834	2	0	Deficient	1937
***Oxyethira novasota* Ross, 1944**	**0**	**1**	**Rare**	–
***Oxyethira obtatus* Denning, 1947**	**0**	**4**	**Rare**	–
Oxyethira pallida (Banks, 1904)	7	102	Abundant	–
Oxyethira serrata Ross, 1938	0	3	Rare	–
***Oxyethira zeronia* Ross, 1941**	**0**	**8**	**Common**	–
Stactobiella delira (Ross, 1938)	1	1	Rare	–
LEPIDOSTOMATIDAE (3)				
***Lepidostoma liba* Ross, 1941**	**3**	**1**	**Rare**	–
Lepidostoma sommermanae Ross, 1946	2	0	Deficient	1980
Lepidostoma togatum (Hagen, 1861)	0	11	Common	–
LEPTOCERIDAE (43)				
Ceraclea alagma (Ross, 1938)	4	12	Common	–
Ceraclea ancylus (Vorhies, 1909)	6	5	Rare	–
Ceraclea annulicornis (Stephens, 1836)	1	1	Rare	–
Ceraclea cancellata (Betten, 1934)	14	19	Common	–
Ceraclea diluta (Hagen, 1861)	6	0	Deficient	1975
***Ceraclea enodis* Whitlock & Morse, 1994**	**0**	**1**	**Rare**	–
Ceraclea flava (Banks, 1904)	3	5	Rare	–
Ceraclea maculata (Banks, 1899)	24	96	Abundant	–
Ceraclea mentiea (Walker, 1852)	1	3	Rare	–
***Ceraclea nepha* (Ross, 1944)**	**0**	**2**	**Rare**	–
Ceraclea ophioderus (Ross, 1938)	1	0	Deficient	1947
Ceraclea punctata (Banks, 1894)	0	4	Rare	–
Ceraclea resurgens (Walker, 1852)	4	0	Deficient	1975
Ceraclea spongillovorax (Resh, 1974)	2	0	Deficient	1974
Ceraclea tarsipunctata (Vorhies,1909)	19	90	Abundant	–
Ceraclea transversa (Hagen, 1861)	19	42	Abundant	–
Leptocerus americanus (Banks, 1899)	20	82	Abundant	–
Mystacides interjectus (Banks, 1914)	4	1	Rare	–
Mystacides sepulchralis (Walker, 1852)	13	23	Abundant	–
Nectopsyche albida (Walker, 1852)	4	9	Common	–
Nectopsyche candida (Hagen) 1861	27	45	Abundant	–
Nectopsyche diarina (Ross, 1944)	14	27	Abundant	–
Nectopsyche exquisita (Walker, 1852)	8	14	Common	–
Nectopsyche pavida (Hagen, 1861)	6	41	Abundant	–
Oecetis avara (Banks, 1895)	7	27	Abundant	–
Oecetis cinerascens (Hagen, 1861)	27	85	Abundant	–
Oecetis ditissa Ross, 1966	8	11	Common	–
Oecetis inconspicua (Walker, 1852)	46	159	Abundant	–
Oecetis immobilis (Hagen, 1861)	9	1	Rare	–
Oecetis nocturna Ross, 1966	14	24	Abundant	–
Oecetis ochracea Curtis, 1825	2	2	Rare	–
Oecetis osteni Milne, 1934	12	3	Rare	–
Oecetis persimilis (Banks, 1907)	7	47	Abundant	–
Setodes oligius (Ross, 1938)	3	2	Rare	–
Triaenodes aba Milne, 1935	1	15	Common	–
Triaenodes flavescens Banks, 1900	3	0	Deficient	1980
Triaenodes ignitus (Walker, 1852)	3	26	Abundant	–

	Records before 1983	Records after 2005	Rarity	Most recent
Triaenodes injustus (Hagen, 1861)	12	50	Abundant	–
Triaenodes marginatus Sibley, 1926	3	34	Abundant	–
Triaenodes melacus Ross, 1947	1	16	Common	–
Triaenodes nox Ross, 1941	3	2	Rare	–
***Triaenodes perna* Ross, 1938**	**0**	**4**	**Rare**	–
Triaenodes tardus Milne, 1934	17	57	Abundant	–
LIMNEPHILIDAE (20)				
Anabolia bimaculata (Walker, 1852)	4	2	Rare	–
Anabolia consocia (Walker, 1852)	7	3	Rare	–
Frenesia missa (Milne, 1935)	5	1	Rare	–
Hydatophylax argus (Harris, 1869)	5	0	Deficient	1980
Ironoquia kaskaskia (Ross, 1944)	1	0	Deficient	unknown
Ironoquia lyrata (Ross, 1938)	1	0	Deficient	1978
Ironoquia punctatissima (Walker, 1852)	3	10	Common	–
Limnephilus indivisus Walker, 1852	8	4	Rare	–
Limnephilus ornatus Banks, 1897	2	0	Deficient	1946
Limnephilus rhombicus (Linneaus, 1758)	1	0	Deficient	1960
Limnephilus submonilifer Walker, 1852	16	4	Rare	–
Platycentropus radiatus (Say, 1824)	9	11	Common	–
Pseudostenophylax uniformis (Betten, 1934)	3	2	Rare	–
Pycnopsyche guttifera (Walker, 1852)	6	14	Common	–
Pycnopsyche indiana (Ross, 1938)	7	30	Abundant	–
Pycnopsyche lepida (Hagen, 1861)	6	5	Rare	–
Pycnopsyche luculenta (Betten, 1934)	4	0	Deficient	1981
Pycnopsyche rossi Betten, 1950	2	0	Deficient	1980
Pycnopsyche scabripennis (Rambur, 1842)	9	3	Rare	–
Pycnopsyche subfasciata (Say, 1828)	15	17	Common	–
MOLANNIDAE (4)				
Molanna blenda Sibley, 1926	2	0	Deficient	1981
Molanna tryphena Betten, 1934	0	7	Common	–
Molanna ulmerina Navas, 1934	3	0	Deficient	1960
Molanna uniophila Vorhies, 1909	10	6	Common	–
ODONTOCERIDAE (1)				
Marilia flexuosa Ulmer, 1905	2	2	Rare	–
PHILOPOTAMIDAE (7)				
Chimarra aterrima Hagen, 1861	10	12	Common	–
Chimarra feria Ross, 1941	3	9	Common	–
Chimarra moselyi Denning, 1948	1	0	Deficient	unknown
Chimarra obscura (Walker, 1852)	8	98	Abundant	–
Dolophilodes distinctus (Walker, 1852)	6	6	Common	–
Wormaldia moesta (Banks, 1914)	4	7	Common	–
Wormaldia shawnee (Ross, 1938)	1	2	Rare	–
PHRYGANEIDAE (11)				
Agrypnia straminea Hagen, 1873	2	0	Deficient	1948
Agrypnia vestita (Walker, 1852)	6	5	Rare	–
Banksiola crotchi Banks, 1943	1	6	Common	–
Fabria inornata (Banks, 1907)	1	0	Deficient	1966
Oligostomis ocelligera (Walker, 1852)	1	0	Deficient	1978
Phryganea cinerea Walker, 1852	1	4	Rare	–
Phryganea sayi Milne, 1931	3	4	Rare	–
Ptilostomis angustipennis (Hagen, 1873)	1	0	Deficient	1950
Ptilostomis ocellifera (Walker, 1852)	7	28	Abundant	–
Ptilostomis postica (Walker, 1852)	4	4	Rare	–
Ptilostomis semifasciata (Say, 1828)	2	9	Common	–

	Records before 1983	Records after 2005	Rarity	Most recent
POLYCENTROPODIDAE (20)				
Cernotina calcea Ross, 1938	0	15	Common	–
Cernotina spicata Ross, 1938	4	24	Abundant	–
Cyrnellus fraternus (Banks, 1913)	17	67	Abundant	–
Holocentropus flavus Banks, 1909	1	0	Deficient	1981
Holocentropus glacialis Ross, 1938	5	4	Rare	–
Holocentropus interruptus Banks, 1914	4	1	Rare	–
Neureclipsis crepuscularis (Walker, 1852)	18	50	Abundant	–
Neureclipsis piersoni Frazer & Harris, 1991	1	2	Rare	–
Nyctiophylax affinis (Banks, 1897)	9	12	Common	–
Nyctiophylax moestus Banks, 1911	5	57	Abundant	–
Plectrocnemia cinerea (Hagen, 1861)	20	48	Abundant	–
Plectrocnemia clinei (Milne, 1936)	0	1	Rare	–
Plectrocnemia crassicornis (Walker, 1852)	2	3	Rare	–
Plectrocnemia nascotius (Ross, 1941)	0	4	Rare	–
Plectrocnemia remotus Banks, 1911	4	2	Rare	–
Polycentropus centralis Banks, 1914	7	24	Abundant	–
Polycentropus chelatus Ross & Yamamoto, 1965	1	0	Deficient	1976
Polycentropus confusus Hagen, 1861	0	12	Common	–
Polycentropus elarus Ross, 1944	1	0	Deficient	1963
***Polycentropus pentus* Ross, 1941**	**0**	**1**	**Rare**	–
PSYCHOMYIIDAE (2)				
Lype diversa (Banks, 1914)	3	42	Abundant	–
Psychomyia flavida Hagen, 1861	3	37	Abundant	–
RHYACOPHILIDAE (6)				
Rhyacophila fenestra Ross, 1938	6	15	Common	–
Rhyacophila glaberrima Ulmer, 1907	1	0	Deficient	1948
Rhyacophila ledra Ross, 1939	5	4	Rare	–
Rhyacophila lobifera Betten, 1934	7	20	Common	–
Rhyacophila parantra Ross, 1948	6	1	Rare	–
Rhyacophila vibox Milne, 1936	1	2	Rare	–
THREMMATIDAE (3)				
Neophylax ayanus Ross, 1938	2	4	Rare	–
Neophylax concinnus MacLachlan, 1871	13	22	Abundant	–
Neophylax fuscus Banks, 1903	3	0	Deficient	1958
Total records	1399	3824		–
Total genera	60	59		–
Total species	191	175		–

Table 2. The seven species listed as occurring in Indiana (Rasmussen and Morse 2023) that should be removed from the state checklist due to misidentified specimens, taxonomic changes, or dubious identification without voucher specimens.

Taxon	Reference	Reason
Cheumatopsyche harwoodi Denning, 1948	Waltz and McCafferty 1983	Misidentified. Specimens are actually *C. analis*
Hydropsyche alvata Denning, 1949	Waltz and McCafferty 1983	Junior synonym of *H. incommoda* (Korecki 2006
Hydropsyche bidens Ross, 1938	Waltz and McCafferty 1983	Junior synonym of *H. incommoda* (Korecki 2006)
Hydropsyche orris Ross, 1938	Waltz and McCafferty 1983	Junior synonym of *H. incommoda* (Korecki 2006)
Hydropsyche rossi Flint et al., 1979	Waltz and McCafferty 1983	Junior synonym of *H. simulans* (Korecki 2006)
Hydropsyche venularis Banks, 1914	Bright (1985)	Larval record without voucher specimens
Pycnopsyche antica (Walker, 1852)	Wojtowicz (1982)	Junior synonym of *P. scabripennis* (Green 2023)

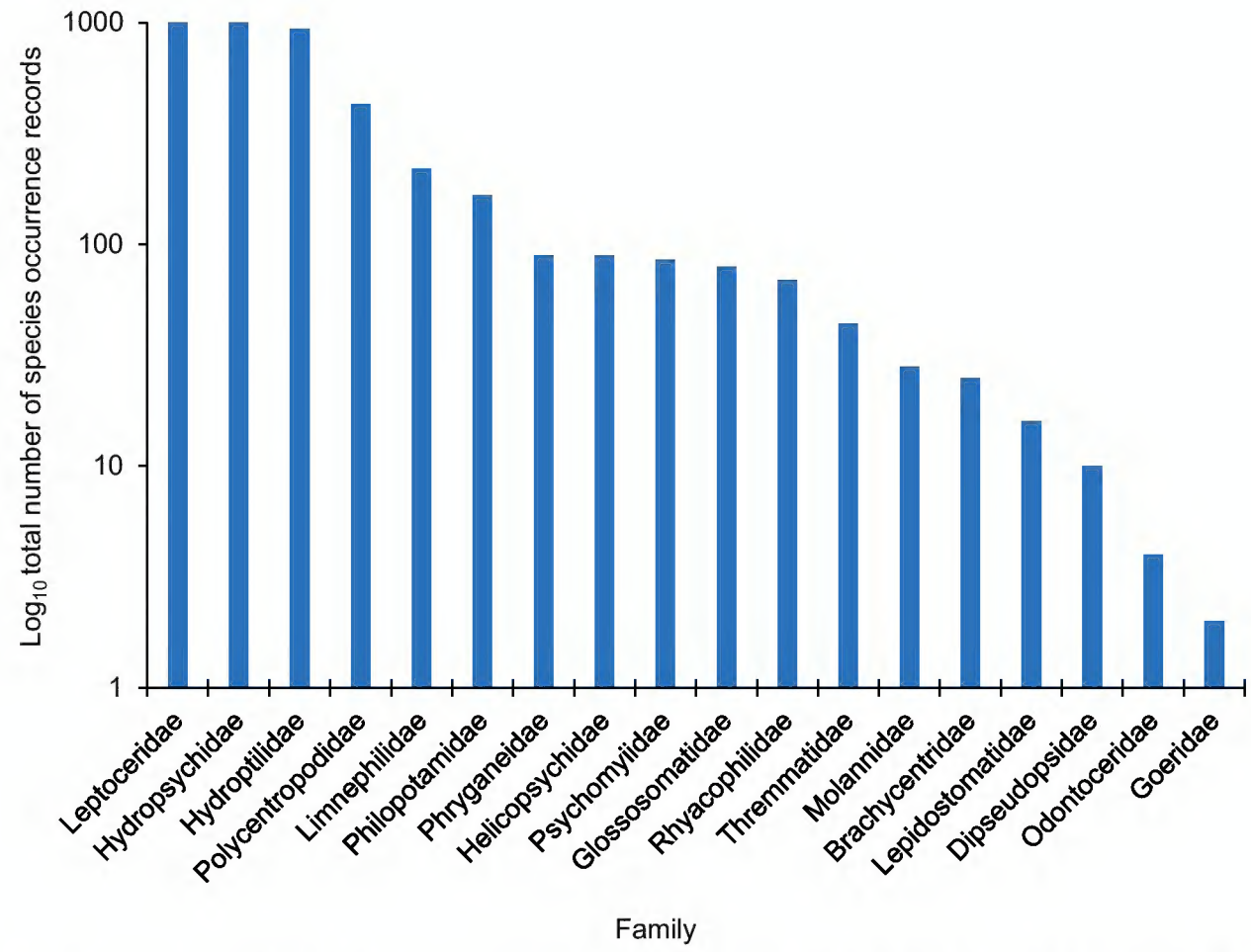

Figure 3. Log_{10} number of species occurrence records for each of the 18 caddisfly families known from Indiana based on all historical and contemporary collecting and sampling.

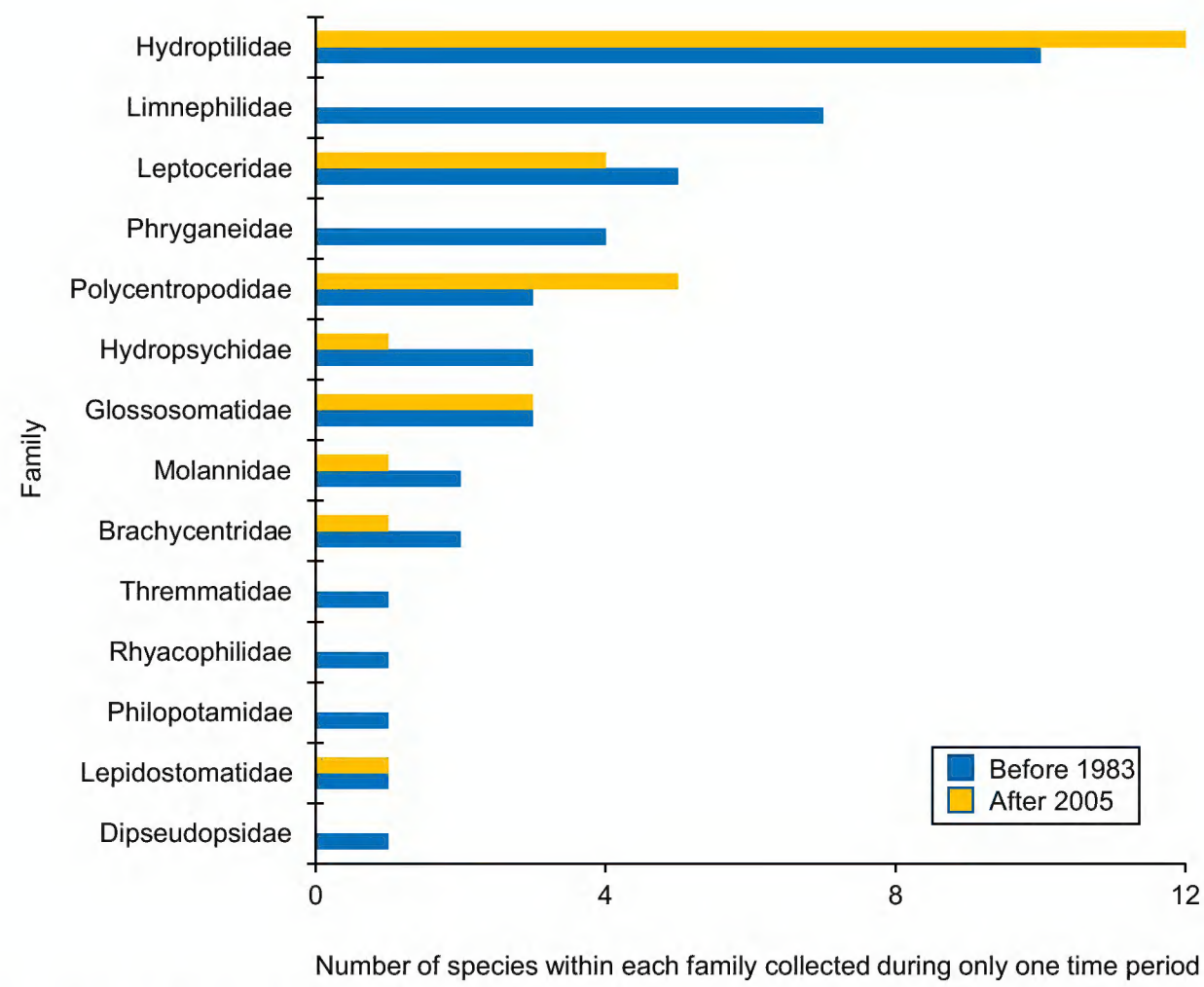

Figure 4. The 72 species collected either before 1983 or after 2005, but not during both periods, organized by family.

On average, species for 12 of the 18 families had an equal or greater number of occurrence records after 2005 than they did before 1983. The exceptions were the Lepidostomatidae (−11%), Phryganeidae (−12%), Thremmatidae (−13%), Molannidae (−31%), Dipseudopsidae (−33%), and Limnephilidae (−42%) (Fig. 5). Similarly, all FFGs had an equal or greater number of occurrence records after 2005 than they did before 1983, except for shredders which decreased by nearly 30% (Fig. 6).

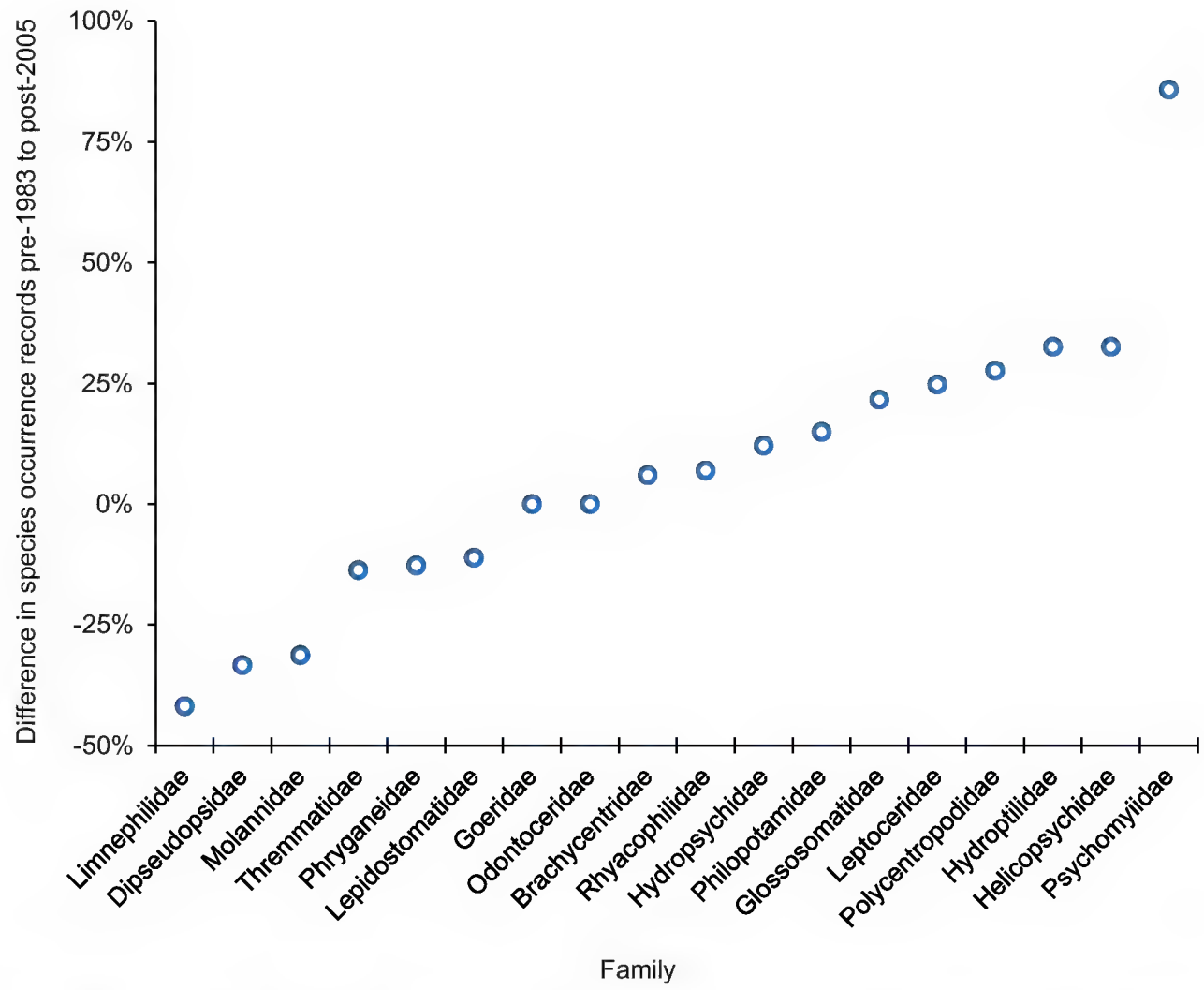

Figure 5. Mean difference between the two time periods of the study in the number of total species occurrence records among the 18 caddisfly families known from Indiana. Difference per species was calculated by subtracting the number of pre-1983 records from the number of post-2005 records and then dividing the result by the total number of records. These values were then averaged to determine the mean difference per family. A positive value signified a greater number of post-2005 records, whereas a negative value signified a greater number of pre-1983 records. Species occurrence data taken from Table 1.

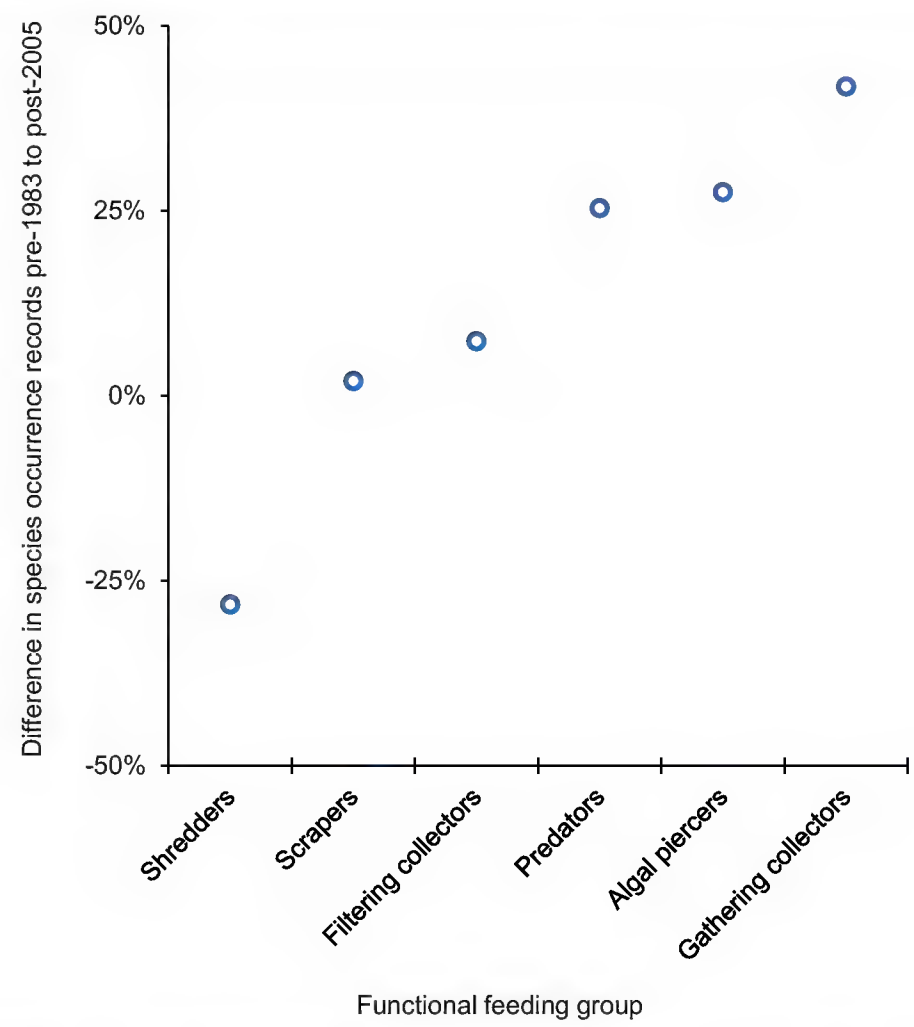

Figure 6. Mean difference between the two time periods of the study in the number of total species occurrence records among the five primary functional feeding groups (FFGs) known from Indiana. Difference per species was calculated by subtracting the number of pre-1983 records from the number of post-2005 records and then dividing the result by the total number of records. These values were then averaged to determine the mean difference per FFG. A positive value signified a greater number of post-2005 records, whereas a negative value signified a greater number of pre-1983 records. Species occurrence data taken from Table 1. FFG data taken from Merritt et al. (2019).

Individual associations between species and the various geographic and habitat designations are in Suppl. material 2 and summarized in Suppl. material 1. Overall species richness differences between the different designations were unremarkable, with the number of unique collecting events being a strong predictor of species richness for both pre-1983 and post-2005 time periods (Fig. 7). Fewer species were caught after 2005 (175) than before 1983 (191) despite having nearly 3× the species occurrence records in the post-2005 time period (Table 1). Total species richness for Indiana was predicted to be 225 and 228 species by ACE and ICE respectively (Fig. 8).

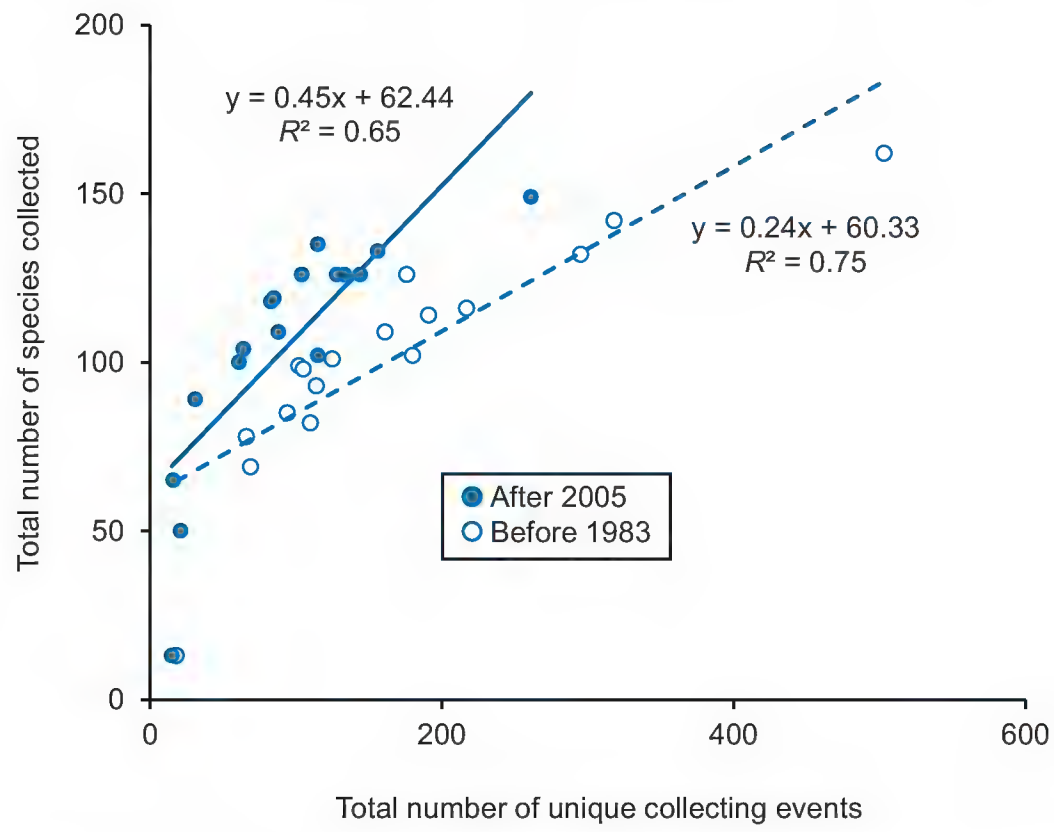

Figure 7. Simple linear regression models of caddisfly species richness (dependent variable) based on the total number of combined collections and samples taken (independent variable) for the two time periods of the study based on all geographic and ecological subunits of Indiana (Suppl. material 2).

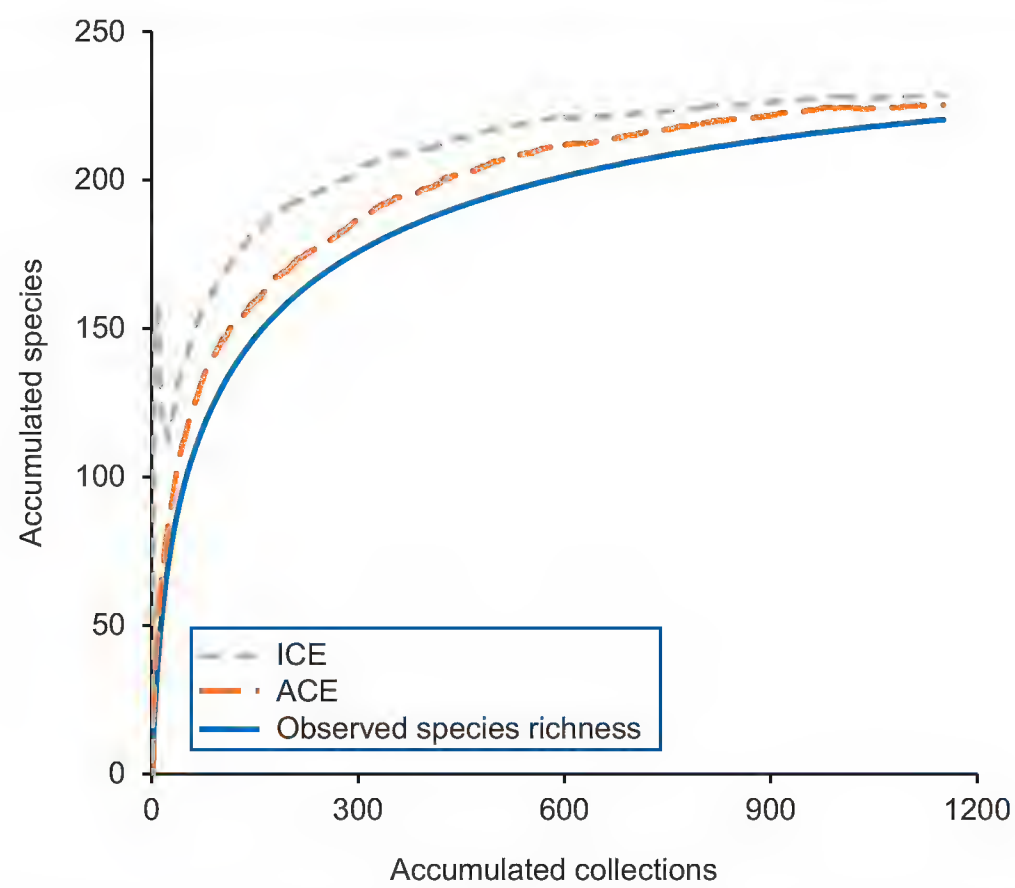

Figure 8. Species rarefaction curves for all historical and recent collections and samples, showing the accumulated number of species and two estimators: the abundance-based coverage estimator (ACE) and the incidence-based coverage estimator (ICE) of actual species richness. For each series, 50 randomized combinations of sample order were calculated and a mean value determined and displayed.

Discussion

Overall species richness within the state was not particularly remarkable or regionally distinctive, which probably reflected a general lack of habitat diversity within Indiana relative to nearby states like Michigan or Wisconsin (Omernik and Griffith 2014). Indiana has no known endemic caddisflies (Rasmussen and Morse 2023). Total species richness of Indiana lagged behind that of the adjacent states of Michigan (319 species), Kentucky (296), Wisconsin (284), and Ohio (276), but was slightly ahead of Illinois (218) (Houghton et al. 2022). Perhaps the most noteworthy difference was the higher richness in the northern half of the state despite having higher agricultural disturbance than the southern half. The Lake Michigan watershed was particularly rich despite having one of the smallest areas. This difference may be due to the high sampling effort of the region. It may also be that the northern portion of Indiana has naturally high species richness due to naturally high groundwater input or its position as an ecotone between prairie and forest (Omernik and Griffith 2014; DeWalt et al. 2016b). In the absence of disturbance, Houghton and DeWalt (2023) predicted the Wisconsin glaciated area in the northern region of the state to have ~1.5× the caddisfly richness per stream than the Illinoian or unglaciated areas. The age of the habitats might also be important, as the more heterogeneous substrates left behind by the recent Wisconsin glaciation probably increased the microhabitat diversity of streams relative to the older eroded landscapes of the Illinoian and unglaciated regions (Benn and Evans 2010).

Differences in caddisfly species occurrence records between the pre-1983 and post-2005 sampling periods indicated the effects of continued habitat degradation in the state. The goal of the current study was to sample the caddisflies with a greater effort than had been done during the pre-1983 sampling period. It is difficult to state definitively that this goal has been accomplished due to the unclear effort of pre-1983 collections; however, the almost 3× greater number of species occurrence records overall and for most families and FFGs in the post-2005 sampling period suggested that it has. Most exceptions were species that were physically large, such as those of Limnephilidae, Molannidae, and Phryganeidae, and in the shredder FFG, such as those of Lepidostomatidae, Limnephilidae, and Phryganeidae. The other two decreasing families, Dipseudopsidae and Thremmatidae have only a few species and, thus, may be more prone to stochastic variation. Houghton and Holzenthal (2010) noted a similar decrease in species occurrence records for large shredders in the Limnephilidae and Phryganeidae in Minnesota. In a study of the Upper Midwest region of the USA, Houghton and DeWalt (2021) observed that >50% of richness loss in shredder species was explained by watershed disturbance, which was more than that of any other FFG. Since shredders are directly dependent on the input of their coarse allochthonous food source, it is expected that they would most directly correlate with intact habitat, especially that of the riparian zone (Houghton et al. 2011; Dohet et al. 2014; Entrekin et al. 2020; Houghton 2021; Williams and Houghton 2024). Moreover, larger caddisfly species in the Limnephilidae and Phryganeidae tend to be uni- or semivoltine (Merritt et al. 2019) and their longer larval period would expose them to habitat disturbances for more time than a multivoltine species would experience. Such a phenomenon has been previously noted for stoneflies in Illinois (DeWalt et al. 2005).

Collection data for new state species records are in Suppl. material 3. The majority of these records are not surprising, as they have previously been found in at least one state adjacent to Indiana. The two notable exceptions were *Agapetus spinosus* Etnier & Way, 1973 and *Protoptila georgiana* Denning, 1948 (both Glossosomatidae). Both of these species were previously thought to be endemic to the southeastern USA, with *A. spinosus* known only from Alabama, South Carolina, and Tennessee, and *P. georgiana* from Alabama, Georgia, Maryland, North Carolina, and Virginia (Rasmussen and Morse 2023). Interestingly, both species were collected from the same site: Marble Creek, downstream of the Big Oaks Wildlife Refuge (BONWR) in Jefferson County (38.8983, −85.4646). The BONWR is one of the least disturbed habitats in Indiana and also one of the least studied, with no known previous collections from it.

Due to the recent sampling effort, most known Indiana species are still presumed extant in the state. Nonetheless, 44 species have not been seen in >40 years and remain data deficient. Eighteen of these species have not been collected in the state since the 1950s and, thus, could have been extirpated by the agricultural development that began after World War II (Omernik 1987). Most notably, *Brachycentrus lateralis* (Say, 1823) has not been seen in Indiana for 121 years.

Future research should include additional sampling. While the species rarefaction curve only predicts a few more species to be found in Indiana, the strong relationship between sampling effort and species caught within the various geographic and habitat designations suggests that a "Wallacean Shortfall" – a lack of detailed data on species distributions (Lomolino 2004) – still remains within the state, and that additional sampling is needed. This shortfall may be pronounced in some autumn-emergent species of Lepidostomatidae and Limnephilidae, due to the difficulty of collecting during the autumn flight period. Since species records for both of these families have decreased since the pre-1983 time period, more autumn sampling is necessary to clarify the reason for this decrease. Conservation efforts in Indiana should probably focus on the 75 rare species, all of which have been collected during the last 2–6 years and are presumed to be extant. Specifically, more information on the life history and specific habitat needs of rare species is necessary to formulate more specific plans for their conservation. Lastly, known or suspected habitats of the 44 data-deficient species should be sampled to ascertain whether these species remain extant in Indiana.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization (DCH), obtaining funding (DCH and RED), sampling (DCH and RED), specimen identification (DCH and RED), data analysis (DCH), manuscript preparation (DCH), manuscript editing (DCH and RED). Both authors contributed to the article and approved the submitted version.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Summary of our collection data by ecological regions and habitat types

Authors: David C. Houghton, R. Edward DeWalt

Data type: xlsx

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Link: https://doi.org/10.3897/zookeys.1216.129914.suppl1

Supplementary material 2

Historical (before 1983), recent (after 2005), and combined species occurrence records for the 219 known Indiana caddisfly species

Authors: David C. Houghton, R. Edward DeWalt

Data type: xlsx

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Supplementary material 3

Specific collection data for the new Indiana state caddisfly species records reported herein

Authors: David C. Houghton, R. Edward DeWalt

Data type: xlsx

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